Mar Biol (2015) 162:2493–2500
DOI 10.1007/s00227-015-2742-5

INVASIVE SPECIES - ORIGINAL PAPER

Forecasting invasions: resource use by mussels informs invasion patterns along the South African coast

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Received: 18 March 2015 / Accepted: 8 September 2015 / Published online: 23 September 2015

Abstract Invasive species are often more able to rapidly and efficiently utilise resources than natives, and comparing per capita resource use at different resource densities among invaders and trophically analogous natives could allow for reliable predictions of invasiveness. In South Africa, invasion by the Mediterranean mussel *Mytilus galloprovincialis* has transformed wave-exposed shores, negatively affecting native mussel species. Currently, South Africa is experiencing a second mussel invasion with the recent detection of the South American *Semimytilus algosus*. We tested per capita uptake of an algal resource by invading *M. galloprovincialis*, *S. algosus,* and the native *Aulacomya atra* at different algal concentrations and temperatures, representing the west and south coasts of South Africa, to examine whether their per capita resource use could be a predictor of their spread and subsequent invasiveness. Regardless of temperature, *M. galloprovincialis* was the most efficient consumer, significantly reducing algal cells compared to the other species when the resource was presented in both low and high starting densities. Furthermore, these findings aligned with a greater biomass of *M. galloprovincialis* on the shore in comparison with the other species. Resource use by the new invader *S. algosus* was dependent on the density of resource and, although this species was efficient at low algal concentrations at cooler temperatures, this pattern broke down at higher algal densities. This was once more reflected in lower biomass in surveys of this species along the cool west coast. We therefore forecast that *S. algosus* will be become established along the south coast; however, we also predict that *M. galloprovincialis* will maintain dominance on these shores.

Responsible Editor: F. Bulleri.

Reviewed by C. L. Griffiths and an undisclosed expert.

This article is part of the Topical Collection on Invasive Species.

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Introduction

As a result of human movement and oceanic global trade, the transport of non-native marine species is occurring across multiple scales and at an increasing rate (Ruiz et al. 1999; Grosholz 2002; Wonham and Carlton 2005; Rilov and Galil 2009; Murray et al. 2014). The subsequent introduction of new species can have significant negative impacts on both the environment and economies of recipient regions (Molnar et al. 2008), in turn resulting in rising mitigation and management costs (Pimentel et al. 2005). In particular, invasive species threaten ecosystem functions and services and threaten native biodiversity (Bax et al. 2003; Simberloff et al. 2013). In general, there is good understanding of invasions with regard to establishment and spread (Parker et al. 1999). For instance, propagule pressure has been found to be reliable predictor of

establishment of a species (Colautti et al. 2006; Simberloff 2009), and invasion history is often valuable for predicting consequences of introductions (Ricciardi 2003; Kulhanek et al. 2011). However, to further such a forecasting capacity, there is a requirement to predict invasiveness and impact from species traits and to understand the associated processes and consequences (Dick et al. 2014).

There have been a number of attempts to assess those invasive species that will be most damaging, with such methodologies often focussing on species trait-based approaches (Sakai et al. 2001; van Kleunen et al. 2010; Keller et al. 2011). In this regard, invasive species are often characteristically more able to rapidly and efficiently utilise resources than native species (Byers et al. 2002; Dick et al. 2013; Alexander et al. 2014). As a result, such invaders may become dominant in the new region if this resource use translates into higher growth rates and/or fecundity (Sakai et al. 2001). Following from this, the comparison of per capita resource utilisation rates and patterns among known invaders at different stages of invasion and trophically analogous natives could allow for more reliable predictions of invader impact (Dick et al. 2014). Similarly, by investigating such per capita resource use under different environmental contexts, such as temperature regimes in potential recipient ranges, predictions may be made of invasion patterns across space and time.

Differential per capita resource use has been attributed to damaging invasive species in a number of taxa and trophic groups (Leffler et al. 2012; Barrios-O'Neill et al. 2013; Alexander et al. 2014); however, it has yet to be applied to invasive filter feeders, in particular bivalves. On rocky intertidal shores worldwide, impacts from invasive bivalves are well documented (Shinen and Morgan 2009) and introduced species can quickly become established, often with serious environmental consequences (Sousa et al. 2009). Impacts that are often linked to such invasions include alterations to space and habitat provision on the shore, which subsequently influence the identity and abundance of co-occurring species (Sadchatheeswaran et al. 2015). Such occurrences have been observed along the west coast of South Africa, where as a result of successive mussel invasions, there have been dramatic changes in the intertidal communities (Robinson et al. 2007; Mead et al. 2011). As such, this system can provide a powerful case study to test whether per capita resource use by invasive mussels when compared to natives can be an effective predictor of mussel invasiveness in this and other regions.

The first mussel introduction to South Africa was the Mediterranean mussel *Mytilus galloprovincialis.* This species has now invaded more than 2000 km of coastline (Robinson et al. 2005) and has become the dominant intertidal organism on many rocky shores since its first detection in the late 1970s (Robinson et al. 2007). The success of *M. galloprovincialis* has been attributed to its rapid growth rate and high reproductive output (Van Erkom Schurink and Griffiths 1991) that has subsequently resulted in declines in the abundance of native species such as the ribbed mussel *Aulacomaya atra* (Branch and Steffani 2004; Branch et al. 2008). Previous work has also indicated that *M. galloprovincialis* has a faster feeding and metabolic rate than a number of native species that is conserved with increased temperature (Van Erkom Schurink and Griffiths 1992). In addition, however, South Africa is now experiencing a second mussel invasion with the recent detection of *Semimytilus algosus,* a native to Chile (de Greef et al. 2013). This invasion appears to have had negative impacts on the South African west coast where the native mussel *A. atra* is rare on many shores (Alexander et al. 2015) and *Choromytilus meridionalis* has been lost on some (Sadchatheeswaran et al. 2015). Furthermore, owing to its smaller maximum size, *S. algosus* has a number of impacts that are distinct from those of *M. galloprovincialis*. These include the exclusion of grazing limpets from monospecific *S. algosus* beds and an increased food source for mussel predators (de Greef et al. 2013). It is also notable that the arrival of this second invasive mussel could have negative consequences for the South African mussel farming industry, as settlement of the smaller *S. algosus* could make this industry unsustainable if the larger *M. galloprovincialis* were to be replaced.

While the range of the established invader *M. galloprovincialis* extends along the whole of the South African west coast and as far as East London on the east coast (Assis et al. 2015), the recent invader *S. algosus* remains constrained to the cool west coast. Moving east past the biogeographic break point of Cape Point, sea temperatures become warmer (Smit et al. 2013) and it is unknown whether *S. algosus* will be able to establish in this region or how it will perform should this occur. Against this background, we selected per capita feeding efficiency in this study to compare the algal resource use capabilities of the two invasive mussels *M. galloprovincialis* and *S. algosus* with the native *A. atra,* in an attempt to assess if this measure would retrospectively have been a suitable predictor of invasiveness in the established invader and whether it may forecast the invasiveness of the newly arrived species. Although a number of other metrics may be measured, we selected per capita resource use as a form of rapid assessment in the way that it has been used in other invasive species prediction studies (i.e. Barrios-O'Neill et al. 2013; Alexander et al. 2014). Specifically, we aimed to: (1) examine whether algal consumption by all three species matches current abundances of the mussels on the west coast; (2) determine whether the documented occurrence of *M. galloprovincialis* could have been predicted by the relative per capita algal consumption of this species; and (3) consider what insight relative per capita algal consumption provides about the potential future invasion of *S. algosus* along the warmer south coast.

Materials and methods

Field surveys: mussel biomass

Seven sites along the west and south coast of South Africa spanning Lamberts Bay in the north to Hermanus in the south were surveyed to determine the relative abundances of *M. galloprovincialis, S. algosus,* and *Aulacomya atra* (Fig. 1). The percentage cover of each mussel species was estimated in the high-, mid-, and low-shore zones at each site using five replicate 0.5 m^2 quadrats. For each mussel species, the mean wet weight of the whole animal supported in three 0.01 m^2 quadrats was taken in 100 % monospecific cover in each zone. This was multiplied by the actual percentage cover recorded, to convert percentage cover to biomass.

A three-factor generalised linear model (GLM) with a quasipoisson distribution was conducted to assess the effects of species (three levels: *M. galloprovincialis*, *S. algosus*, *A. atra*), site (seven levels: Lamberts Bay, Elands Bay, Marcus Island, Bloubergstrand, Hout Bay, Hangklip, Hermanus), and shore height (three levels: high-, mid-, low shore) on biomass.

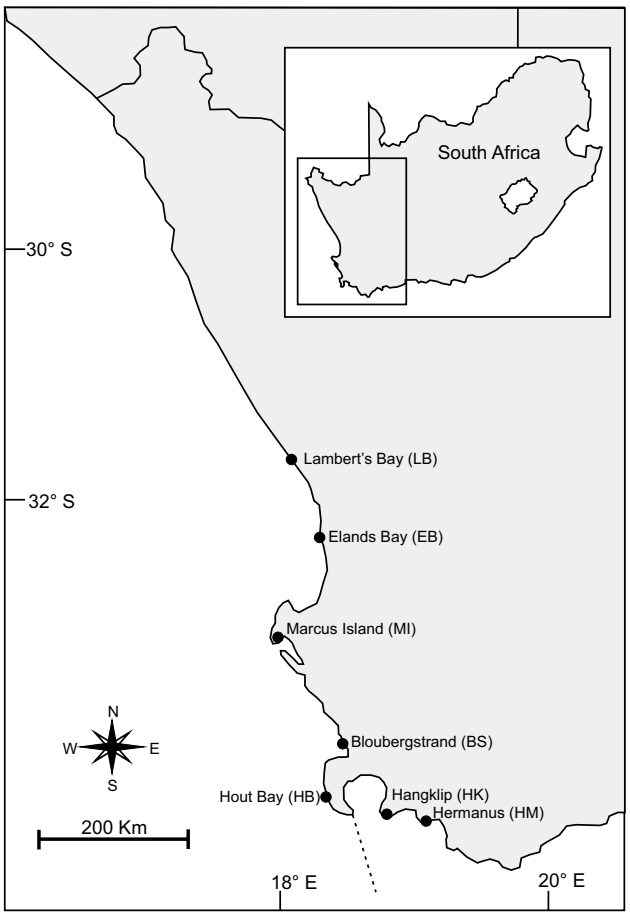

Fig. 1 West coast of South Africa indicating the seven sites surveyed for mussels. *Dashed line marks* the biogeographic break between the Southern Benguela and the Agulhas ecoregions at Cape Point

Laboratory experiments: comparison of algal consumption

In austral winter of 2014, body size-matched individuals of each mussel species, measuring 2 ± 0.2 cm in length, were haphazardly collected from Bloubergstrand (−33.796767°S, 18.462082°E) and Hout Bay (−34.048609°S, 18.360457°E) on the west coast. Mussels were returned to the laboratory and placed in holding tanks with continuously aerated artificial seawater maintained at 15 °C and 28–32 ppt salinity. Seawater in the holding tanks was changed every 2–3 days, after which mussels were fed a phytoplankton suspension ad libitum of *Isochrysis* and *Pavlova* spp. with a cell size range of 4–10 µm. As given shell length can represent different investments in terms of body mass in mussel species (Van Erkom Shurink and Griffiths 1993), we compared mussel body mass from this size range of the three mussel species. Flesh was removed from 15 representative individuals of each species and blotted dry before weighing to three decimal places. Mussel body mass did not differ significantly among species ($F_{2,42} = 0.611$, $p = 0.5$).

The per capita algal consumption by the three species of mussel was quantified at two temperatures that are representative of the west (13 °C) and south coasts (20 °C) of South Africa (Smit et al. 2013). Mussels were acclimated to the appropriate temperature for 48 h prior to experimental trials. At each of the two temperatures, eight groups of five mussels from each species were randomly selected from holding tanks and allocated to experimental pots (10 cm diameter). Groups of mussels instead of individuals were used to aid detection of algal consumption. These pots were filled with 500 mL seawater for 48 h prior to the addition of algae to allow acclimatisation to the arena as well as standardisation of mussel starvation levels. Of the eight groups of each species, four were randomly allocated to low algal concentration feeding trials and four to high concentration trials. After the acclimation period, the mussels were provided with either a low (1×10^6 cells/L) or a high (32×10^6 cells/L) algal concentration addition to reflect the differential productivity of the south and west coasts, respectively. Algae supplied were the same phytoplankton suspension on which the mussels were maintained. The appropriate volume of water was removed just prior to this addition to ensure that total water volume in the tank did not change when algal treatments were added. Mussels were allowed to feed for 1 hour before three 1 ml samples of water were removed and placed in Eppendorf

tubes before being transferred immediately into dark conditions. The concentration of algal particles in these samples was determined using flow cytometry.

Data from each algal concentration (i.e. low and high) were analysed separately as the statistical main effect of algal concentration was rather meaningless (i.e. mussels filter more when more is available) and inclusion of this main effect made the other main effects and their interactions less tractable. The concentration of algal cell remaining at the end of one-hour filtration time for both low and high initial algal concentrations was thus examined with respect to mussel species (three levels: *M. galloprovincialis*, *S. algosus*, *A. atra*) and temperature (two levels: 13, 20 °C) in separate two-factor GLMs, with quasipoisson error distributions.

Table 1 GLM results of mussel biomass with respect to species (three levels), site (seven levels), and shore height (three levels)

Source of variation	df	Deviance	*F*	*p*
Species	2	1754.21	877.11	<0.001
Site	6	207.57	34.59	<0.001
Shore height	2	443.11	221.55	<0.001
Species × site	12	152.53	12.71	<0.001
Site × shore height	12	130.20	8.58	<0.001
Species × shore height	4	30.25	7.56	<0.05
Species × site × shore height	24	89.51	3.73	<0.001

Results

Mussel biomass

Overall, there was a significant effect of 'species' on biomass ($F_{2,304} = 877.11$, $p < 0.001$; Table 1; Fig. 2), with *M. galloprovincialis* supporting greatest biomass, followed by *S. algosus* and then *A. atra* (all pairwise comparisons $p < 0.001$; Fig. 2). There was also a significant effect of 'site' ($F_{6,308} = 34.59$, $p < 0.001$; Table 1; Fig. 2) with Hangklip (HK) supporting less mussel biomass in comparison with Elands Bay (EB), Bloubergstrand (BB), and Hermanus (HM; all pairwise comparisons $p < 0.05$; Fig. 2). Total biomass of mussels increased significantly down the shore, with particularly reduced biomass on the high shore ($F_{2,306} = 221.55$, $p < 0.001$; Table 1; Fig. 2). The significant 'species x site' interaction ($F_{12,280} = 12.71$, $p < 0.001$; Table 1; Fig. 2) was driven by relatively high biomass of *S. algosus* only at Elands Bay (EB), Bloubergstrand (BB), and Hout Bay (HB) and relatively low biomass of *M. galloprovincialis* at Hangklip (HK),

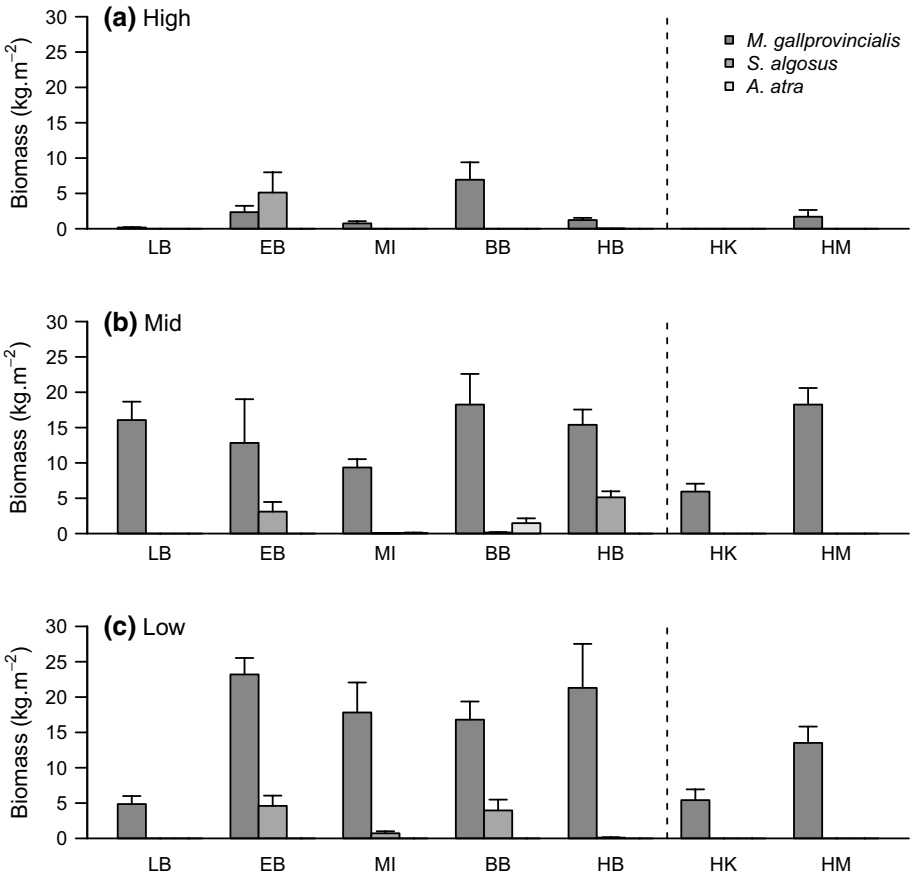

Fig. 2 Mean biomass (kg/m^2; +SE) of *M. galloprovincialis, S. algosus,* and *A. atra* in the **a** high-, **b** mid-, and **c** low shore at Lamberts Bay (LB), Elands Bay (EB), Marcus Island (MI), Bloubergstrand (BS), Hout Bay (HB), Hangklip (HK), and Hermanus (HM). *Dashed line marks* break between west coast and south coast sites

with rarity of *A. atra* across sites. The singificant 'site x shore height' interaction ($F_{12,292} = 8.58$, $p < 0.001$; Table 1; Fig. 2) was driven by some sites [e.g. Lamberts Bay (LB)] increasing and then decreasing in mussel biomass from high to low shore. The 'species x shore height' interaction ($F_{4,276} = 7.56$, $p < 0.001$; Table 1; Fig. 2) was driven by *S. algosus* appearing at more sites on the mid- and low shore and *A. atra* appearing only on the mid-shore. These complex patterns were reflected in the three-way 'species × site × shore height' interaction ($F_{24,252} = 3.73$; Table 1; Fig. 2).

Algal consumption

Under low algal concentrations, there was a significant effect of 'species' on the number of algal cells remaining ($F_{2,20} = 17.76$, $p < 0.001$; Fig. 3a) and this was driven by significantly fewer cells remaining in the *M. galloprovincialis* treatment in comparison with *A. atra* (Tukey's post hoc, $p < 0.05$) with *S. algosus* intermediate in the number of cells remaining. There was a significant effect of 'temperature' on the algal cells remaining ($F_{1,19} = 41.26$, $p < 0.001$; Fig. 3a), with significant reductions in the 13 °C treatments in comparison with 20 °C for both *S. algosus* and *A. atra* (Tukey's post hoc, $p < 0.01$). There was no significant 'species × temperature' interaction. In the high algal concentrations, there was again a significant effect of 'species' on the number of algal cells remaining ($F_{2,20} = 9.51$, $p < 0.01$; Fig. 3b), which was once more driven by significant reductions in algal cells by *M. galloprovincialis* compared to *A. atra* (Tukey's post hoc, $p < 0.05$), with *S. algosus* again intermediate in the number of cells remaining. As in the low algal concentration trial, significantly fewer algal cells remained overall in the 13 °C treatments in comparison with 20 °C ($F_{1,19} = 7.04$, $p < 0.05$; Fig. 3b), however, there were no significant differences in algal cells remaining between temperatures for any of the species. There was no 'significant species × temperature' interaction.

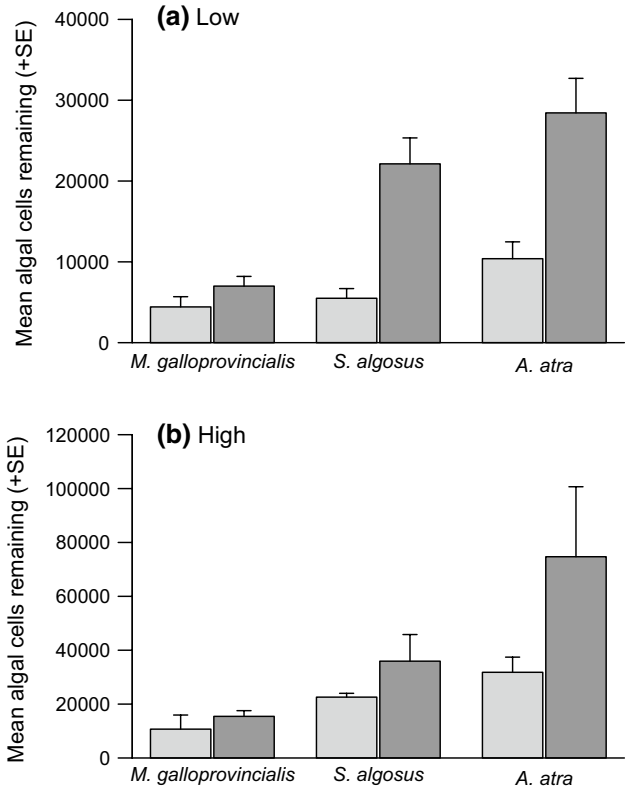

Fig. 3 Mean number (+SE) of algal cells remaining after 1 h of filtration by *M. galloprovincialis*, *S. algosus,* and *A. atra* at **a** low and **b** high concentrations of algae at 13 °C (*light grey bars*) and 20 °C (*dark grey bars*)

Discussion

The global rate of biological invasions in marine systems is accelerating (Bax et al. 2003; Molnar et al. 2008; Rilov and Galil 2009), and there is a pressing requirement to improve our ability to predict those species that are likely to be highly invasive and result in deleterious ecological impacts (Parker et al. 1999; Dick et al. 2014). As such, it has been recognised that comparing relative per capita resource use between damaging invasive species, emerging invaders and comparator natives may be an effective tool in predicting and explaining invasiveness and subsequent impact (Barrios-O'Neill et al. 2013; Alexander et al. 2014; Dick et al. 2014). In the present study, we examined comparative per capita resource use of three mussel species in South Africa, the established invader *Mytilus galloprovincialis,* the more recent invader *S. algosus,* and a native species *A. atra.* Our field surveys showed that *M. galloprovincialis* is the dominant mussel along the west and south coast, with *S. algosus* occurring at intermediate densities at certain sites, and the native species now very rare. We found that resource use in the laboratory aligned with these patterns, observing significantly increased per capita algal resource use by *M. galloprovincialis* in comparison with the other two species at two temperatures and two resource densities.

The west coast of South Africa typically experiences cooler water temperatures in comparison with the south coast owing to the wind-driven Benguela upwelling regimes (Branch and Griffiths 1988). In our laboratory experiments that tested relative per capita algal consumption between the three mussel species at temperatures that represented these colder conditions (13 °C), it was found that *M. galloprovincialis* was the most efficient consumer of the algal food resource. This was evidenced by significant reductions compared to the other two species in the number of algal cells remaining after an hour filtration time, which was observed under both low and high

resource densities. These findings not only align with the biomass surveys, but also corroborate known field impacts of the species where it is the dominant mussel along much of the shore line, occurring at the expense of other species (Steffani and Branch 2005a, b). This heightened per capita resource use efficiency suggests a competitive advantage that supports the species ability to outperform native species in terms of growth rate, reproductive output and tolerance to desiccation (Van Erkom Shurink and Griffiths 1993). These results also align with previous work that compared respiration, ammonia excretion, and absorption efficiency of *M. galloprovincialis* to three native species (Van Erkom Shurink and Griffiths 1992).

Although resource use by *M. galloprovincialis* under the cooler temperatures was consistently efficient in comparison with the other mussel species at both low and high algal concentrations, the patterns observed in *S. algosus* were dependent on the density of the resource that was available. While at low algal resources, under colder temperatures, there were a comparable number of algal cells remaining in *S. algosus* compared to *M. galloprovincialis* treatments, this pattern broke down at high resource levels and the per capita filtration capabilities of the recent invader were more closely aligned to those of the native *A. atra*. In addition to evidence suggesting that filtration rates may be influenced by temperature (Schulte 1975; Fanslow et al. 1995; Haure et al. 1998), mussels can also change their filtration and ingestion rates with resource availability, with maximum filtration rates occurring at low resource densities (Newell et al. 2001). It appears here that both invasive species are maximising their filtration capabilities at these lower algal concentrations, a characteristic often observed in invasive species (Dick et al. 2014). The reduced feeding rate in *S. algosus* at higher resource availability, however, may suggest the occurrence of a threshold resource concentration level, which, once surpassed, results in declines in feeding efficiency. Such a phenomenon has been shown to vary among species and may result in less algae being removed in comparison with *M. galloprovincialis* at these higher resource levels (Riisgard et al. 2003; Filgueira et al. 2009). It may therefore be deduced that different species can show variable responses to differing food concentrations and it appears here to be temperature dependent. When considering overall feeding, over a range of algal concentrations, these findings suggest that *S. algosus* is not as efficient a per capita consumer as the more established invader under these cooler, west coast conditions. Once again, these results were echoed in *S. algosus* having a lower biomass on the shore.

These findings may have been influenced by the standardisation of mussel size (2 cm length) used in the filtration experiments. This is in contrast to the shore survey that considered biomass of all size classes. Therefore, in our experiments, biomass was essentially constant between the species allowing us to detect per capita species differences rather than size differences. When these per capita differences are extrapolated to the field, however, it is considered that differential filtration capabilities will become more pronounced. This is due to faster growth rates of *M. galloprovincialis* over time in comparison with *A. atra* (Van Erkom and Griffiths 1993) that correlate with higher filtration rates, absorption efficiencies, and respiration (Van Erkom and Griffiths 1992). Although in colder temperatures *S. algosus* was more efficient than the native *A. atra* in algal uptake capability, this was not matched quite to the same degree on the shore in terms of biomass. As already noted, this might be a reflection of the recent invasion of *S. algosus*. However, adult *M. galloprovincialis* are larger than adult *S. algosus* (authors personal observation) and, as size-matched *M. galloprovincialis* individuals outperformed this species in the laboratory, it is expected that the larger individuals in the field would hold an even greater advantage (Van Erkom and Griffiths 1993). This may partially explain why greater differences were recorded between the abundance of the species in the field than were suggested by our filtration experiments.

The presence of *S. algosus* in Hout Bay is indicative of a southward range extension of more than 50 km since 2010 (de Greef et al. 2013); therefore, the new invader is in fact moving southwards and close monitoring is required to chart any further spread that may occur. Although Cape Point is considered a biogeographic break point, owing to prevailing offshore currents that limit many species distributions (Awad et al. 2002), near shore currents may move in a southerly direction (Nelson and Polito 1987). There is, therefore, potential for larval transport that could enable the spread of *S. algosus* around the peninsula to the warmer waters of the south coast, although our surveys on the south coast sites have not yet detected the presence of this species. Our results suggest that if *S. algosus* were able to pass this break, either naturally or through human-mediated transport, then it would likely become established. However, under such warmer conditions, at both low and high algal densities, we found *M. galloprovincialis* to outperform *S. algosus* in filtration capabilities. This finding linked with a high growth and fecundity rate, suggests that *M. galloprovincialis* would remain the dominant mussel species along this coast.

It is important to note that even although the differential per capita ability of species to consume food resources may indicate which species is likely to be dominant (Miller et al. 2005), the limiting resource for mussels in a rocky shore environment is unlikely to be food. This is particularly true on the west coast of South Africa which is characterised by strong upwelling and high productivity (Bosman et al. 1987; Lucas et al. 2014). Subsequently, the limiting

resource on rocky shores may in fact be space, where mussels and other intertidal organisms compete for primary rock space (Dayton 1971). The dominance of mussels may therefore be dependent on such species being able to utilise mechanisms allowing them to compete for space; however, it is expected that feeding performance will be tightly linked to such processes. For example, at moderately wave-exposed sites *M. galloprovincialis* has been shown to occur in high densities, with rapid growth rate and an increased condition index (Steffani and Branch 2003). Such features, coupled with intraspecific processes such as self-thinning, allow mussel species to preempt rock primary space and therefore maintain high densities and local dominance on the shore with significant impact on native communities (Branch et al. 2008, 2010).

A further consideration is the use of other metrics that may be appropriate for testing the questions that we set out to address here. Filtration rates are tightly coupled to other physiological processes such as respiration rates and absorption efficiency (Van Erkom Schuring and Griffiths 1992), and growth rates related to water circulation and tidal exposure (Van Erkom Schuring and Griffiths 1993) may have important implications for the invasiveness and subsequent impact of an invading species. However, the approach we utilised here was in line with previous work that has investigated heightened per capita resource use in a laboratory setting which corroborates with negative field impacts (Barrios-O'Neill et al. 2013; Alexander et al. 2014).

This study has applied a comparative per capita resource use concept to examine whether the invasions by two species of mussel, *M. galloprovincialis* and *S. algosus*, along the west coast of South Africa could have been predicted based on per capita algal uptake as compared to a native species, *A. atra*. We found that such resource use in the laboratory, heighted in *M. galloprovincialis*, aligns with the field biomass surveys and would have been a reliable indicator of the spread and subsequent establishment of this species. In addition to this, we predict, based on the per capita reduction in algal cells under south coast conditions, that *S. algosus* will likely spread along the coast if it surpasses the biogeographic break at Cape Point. We also expect, however, that *M. galloprovincialis* will hold its competitive edge along the coastline and remain the dominant intertidal mussel species in South Africa. We have therefore further shown, using South African mussel invasions as a case study, the applicability of comparative per capita resource use (see Dick et al. 2014) in the prediction of invasiveness and identification of non-native species that are likely to have deleterious ecological impacts.

Acknowledgments We would like to thank H. Raven, S. Sadchatheeswaran and G. and M. Branch for assistance in field sampling, and R. Adams at the Centre of Analytical Facilities, Stellenbosch University, for assistance with flow cytometry. This study was funded by the DST-NRF Centre of Excellence for Invasion Biology.

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